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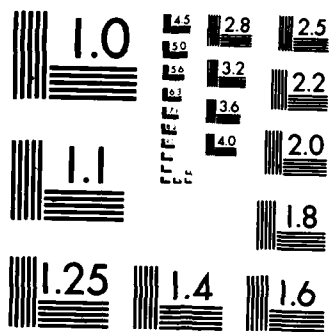


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A conference was organized that brought together 133 research scientists of diverse specialities to address a comprehensive review of the experimental and theoretical advances in color vision and to consider their application to the design of color-coding and color displays.		

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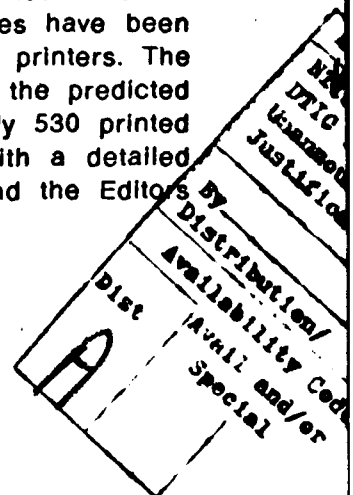
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'COLOUR VISION: PHYSIOLOGY AND PSYCHOPHYSICS'

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(c)The meeting was very successful in bringing together scientists from different specialities and different continents, and genuinely fruitful discussions were engendered between people who otherwise would have been unlikely to meet.

It is our hope, and that of the publisher, that the book resulting from the meeting will serve as a unique handbook to current research on color vision and will be more useful than a typical volume of conference proceedings. Among the topics of especial interest are: the first electrophysiological measurements from single primate photoreceptors; new and extensive microspectrophotometric measurements of human and primate cones; the first microspectrophotometric measurements from a human deuteranope; the presence of several dichromatic and trichromatic forms of color vision within a single primate species; electrophysiological recordings from single cells in the retina, lateral geniculate nucleus and visual cortex; effects of selective environments on the development of color vision; psychophysical measurements of thresholds for detection and discrimination; color constancy; and color coding.

Color vision was once a field of rather bitter controversy. This tradition was not in evidence at the Cambridge meeting, owing probably to the existence now of a common corpus of agreed knowledge. Thus there was no dispute about the number of types of retinal receptor and the gross spectral positions of their peak sensitivities (430, 530 and 560 nm) and it is equally agreed that there exist higher-order cells that receive signals of opposite sign from these receptors, thus allowing wavelength information to be extracted by the visual system. However, several areas of current dispute were identified at the meeting and are discussed in the book: Are there variations between normal observers in the wavelengths of peak sensitivity of their photoreceptors? Are there separate post-receptoral channels for chromatic and spatial information, as has been held for the past decade, or do the same fibres in the visual pathway carry information about both hue and spatial detail, as several authors now suggest? Are there areas of visual cortex that are specialized for the analysis of color, as proposed by S. Zeki (In the present book Zeki's claim is supported by Guld, Anderson and Sjo from Copenhagen, and opposed by Kruger and Fischer from Freiburg). Why is our vision so odd when it depends on signals originating only in the short-wavelength receptors? (With respect to this question, the meeting revealed widespread agreement that part of the answer lies in the low numerosity of the short-wave receptors: several independent estimates suggest that they constitute less than 10% of all retinal cone cells.)

J. D. Mollon  
February, 1983

## PREFACE

We live in a world that is increasingly colour-coded. Not only are colours used for differentiation in technical fields such as electronics, transport signalling and military identification, but also the general public are daily exposed to colour coding in drugs, road signs, maps of transport systems and of large buildings, commercial packaging, advertising logos, teaching materials, and teletext systems. Colour visual-display-units are about to come into widespread use. Thus there are today strong practical reasons why we should improve our understanding of what limits our capacity to differentiate wavelengths, of how the neural analysis of colour is related to that of other attributes of the visual stimulus, and of why some 8% of the male population are deficient in colour discrimination.

Colour vision has never been the private preserve of any single one of the conventional disciplines of science. Its subtle but lawful complexities have attracted physicists, experimental psychologists, physiologists, ophthalmologists and optometrists. To this day, colour scientists are scattered among many different types of institution and their publications are similarly distributed among a variety of journals. In August 1982 an international meeting was held at Cambridge with the explicit purposes of bringing together colour specialists from different disciplines and of preparing the present handbook. It was the organisers' intention that the book should cover all aspects of colour vision, from the retinal photopigments to sensation; that equal weight should be given to physiological and psychophysical results; and that tutorial material should be included in order to introduce specific research problems and techniques to the non-specialist. We have concentrated on man - and on his primate relatives, who, it now seems, provide close models for both normal and deficient human colour vision.

Those who study colour vision are conscious that it is a field with a past. Much can be deduced about colour vision by purely sensory experiments in which an observer is asked to say whether two physically different lights appear alike or different; and the results have lent themselves to elegant geometrical analyses. Consequently, in the last three centuries, the problems of colour vision have engaged the attention of some of the most distinguished of natural scientists. It was fitting therefore that present meeting should be held at the University of Cambridge, the university of Newton, Thomas Young, Clerk Maxwell and Lord Rayleigh. Indeed, for many at the meeting, the beginnings of modern colour science were betokened by a holograph notebook (lent for display by the Fitzwilliam Museum) in which Newton recorded his purchase in 1667 of three prisms for three shillings. In an Appendix to the present book we have included the text of two talks given in conjunction with the meeting - an account by F. W. Campbell of Cambridge contributions to colour science; and a memoir by M. Alpern of the Cambridge physiologist W. A. H. Rushton.

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Cambridge last saw an international meeting on colour vision in 1947. The proceedings of that meeting (Documenta Ophthalmologica, vol 3, 1949) still repay careful reading; but we now enjoy an agreed corpus of physiological knowledge that was not available thirty-five years ago. In 1947 the spectral sensitivities of the photoreceptors, and indeed the number of types of photoreceptor, were matters for wide disagreement. No electrophysiological recordings were available from single cells in the primate visual system. Today, though they might make local qualifications, most colour scientists would agree on the following account of the early stages of colour analysis in the human visual system:

Our sensations of hue depend upon the relative rates of absorption of photons in three classes of retinal photoreceptor, which have peak sensitivities at wavelengths of approximately 560 nm, 530 nm and 420-430 nm. The short-wavelength receptors are rarer than the long- and middle-wavelength receptors. The spectral sensitivities (i.e. the curves that relate sensitivity to wavelength) of the different classes of receptor are broad and overlapping and the electrical signal of an individual receptor preserves no information about the wavelength of the light that is being absorbed. So, in order that the visual system should be able to separate changes in colour from changes in intensity, some post-receptor neurons receive inputs of opposite sign from different classes of photoreceptor. Among retinal ganglion cells and among the cells of the parvocellular layers of the lateral geniculate nucleus, there are two main classes of these 'colour-opponent' neurons. The most common type receives an input of one sign (excitatory or inhibitory) from the long-wavelength receptors and an input of the opposite sign from the middle-wavelength receptors; this type of neuron is also spatially opponent in that the two inputs are drawn from spatially distinct regions of the receptor array, a disc-shaped central region and a concentric surround. A somewhat rarer type of colour-opponent neuron receives an input of one sign from the short-wavelength receptors and an input of opposite sign from the long- and middle-wavelength receptors; in this case the excitatory and inhibitory inputs are drawn from the same disc-shaped area of the receptor array. The reader will be able to add flesh to this skeleton by referring to Sections I and IV of the present book.

On one central issue the present book probably marks a turning point. Thirty-five years ago colour scientists were concerned to develop psychophysical techniques for isolating the responses of individual classes of receptor - by removing other classes of receptor from play by means of monochromatic adapting fields, or by choosing spatial and temporal parameters that favoured one class, or by choosing observers who lacked one or more class. About eight years ago interest began to shift to psychophysical techniques for isolating different types of post-receptor channel. Thus it seemed that a liminal target was likely to be detected by 'chromatically opponent' channels if the target was of large area and long duration and if an achromatic adapting field was present. Under such conditions the spectral sensitivity of the eye has multiple peaks (one of which lies at a wavelength much longer than the wavelength of peak sensitivity of the long-wavelength receptors); and when targets, or adapting fields, of different

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wavelengths are combined, the effect of the combination may be less than predicted by simple additivity. On the other hand, if a target is small and brief and if a monochromatic adapting field is present, then it may seem that detection is mediated by a 'non-opponent' pathway: the spectral sensitivity of the eye has a single peak and additivity is often found to hold. The dichotomy between 'opponent' and 'non-opponent' channels has proved a very fruitful concept in recent research and the reader will find that it is discussed, in various forms, in several papers in the present volume. Equally, however, the reader will find an increasing realisation that the psychophysicist's dichotomy has never agreed with the physiological knowledge outlined in the preceding paragraph: the same retinal ganglion cell may apparently signal either local achromatic contrast or the presence of homogeneous colour. The psychophysicist's 'channels' may represent the same cells operating in different modes; and central mechanisms may have to consider the output of a population of cells in order to separate spatial and chromatic information. On this issue, see especially papers 17, 35 and 39.

Some other recurrent issues can be identified in the pages that follow. Are there variations between 'normal' observers in the spectral positions of their photopigments (see papers 2, 4, 5 and 7)? Are the colour-specific neurons of the visual cortex grouped into 'columns' (papers 25 and 26)? Are there areas of prestriate cortex that are specialised for the analysis of colour (papers 26 and 27)? Why is our vision so odd when discrimination depends only on signals originating in the short-wave receptors (papers 40, 44-48)? What is the relation between, on the one hand, the opponent processes revealed by measurements of thresholds and, on the other, the phenomenological antagonism of particular pairs of hues (papers 33, 34, 35, 36 and 54)? How do we recognise the spectral reflectances of objects despite large changes in the spectral composition of the illuminant (papers 49 and 50)?

Very recently, colour vision research has found a new tool in the form of the computer-controlled colour television monitor. Raster displays of this type allow the generation of colour stimuli that vary elaborately in space, in time, and in chromaticity; but such displays have to be selected and used with care and we have therefore included two tutorial papers (11 and 12) that describe not only the versatility but also the limitations and pitfalls of computer-controlled displays. Specific uses of raster displays are illustrated in a number of other papers (13, 14, 21, 38, 40, 42, 49 and 51).

The papers included in this volume have been refereed. The editors and referees have deliberately not sought to impose a common theoretical approach on the papers selected for inclusion, but, in the brief time available, have tried merely to eliminate obvious non-sequiturs, internal inconsistencies, and obscurities of expression. We have not attempted to impose British spelling on our American colleagues. Since we hope that the book may provide bibliographic access to the scattered literature on colour vision, we have taken particular trouble to check references. We thank all the contributors for their helpfulness during the editing

process.

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Throughout the planning of the meeting and the editing of this book we have been guided by an international committee consisting of Professor C.R. Cavonius (Dortmund), Dr. O. Estevez (Amsterdam) and Dr. J. Krauskopf (Murray Hill, NJ). We most sincerely thank these colleagues for their help. We have been indebted to Betty Clifton for secretarial assistance during the organisation of the meeting and the preparation of the book. We also wish to thank Professor N. J. Mackintosh and Professor R. D. Keynes for providing facilities for the meeting; Trinity College, Cambridge, for its hospitality to our delegates; and Mr. C. Hood for several kindnesses at the time of the meeting.

J. D. Mollon, L. T. Sharpe

Cambridge, January, 1983

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